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THE PLANT ECOLOGY OF THE
GRAHAMSTOWN NATURE RESERVE:

II. SOME EFFECTS OF BURNING

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INTRODUCTION

In part I of this study (Martin 1964) a general account of the vegetation of the Reserve has described the domination of the area by nanophanerophyte (ericoid) heath, temperate tussock grassland and temperate evergreen rain-forest formations.

In an attempt to preserve part of this flora near Grahamstown, the Reserve has been cleared, in the main, of exotics such as Pines, Australian Wattles, *Hakea* and Bluegum, fenced and surrounded by firebreaks 12 ft. wide. These firebreaks have not prevented veld fires entering the Reserve. One such fire occurred in August, 1948, during a period of intense drought, which persisted until 1949. A comparison of the phenological response of species on burnt and unburnt ericoid heath and grassland was commenced, in order to throw some light on the secondary plant succession. These observations were supplemented by the experimental burning of small plots to study the physical conditions during fire and the differences observable after burning when the composition of the vegetation was more accurately known.

During these studies a second fire, in August, 1951, burned a good deal of the heath missed by the earlier fire. This burning was followed by a wet spring and considerable differences in response of some species were noticed. Observations, including some soil studies, were continued through 1952.

In 1955 a very severe fire destroyed almost all the remaining heath in the Reserve together with the regenerative growth in the previously burned areas, and so altered the conditions of succession that the original objects of the investigation were at least partly nullified. Nonetheless, observation till September, 1956, gave some additional information and the work as a whole, though somewhat incomplete, forms a report on the state of the Reserve and a basis for more detailed research.

THE REGENERATION AND FLOWERING OF SPECIES IN ERICOID HEATH FOLLOWING FIRES

Observations of vegetative regeneration and flowering times, and qualitative estimates of flowering abundance were made after each burning. Owing to some contrasts in regenerative behaviour between dry and moist conditions, the periods of observation are best considered separately.

(a) The Fire of 1948.

(1) PHENOLOGY.

Phenological observations made between 1948 and 1951 suggested that regenerating plants could be placed in five groups (Table 1).

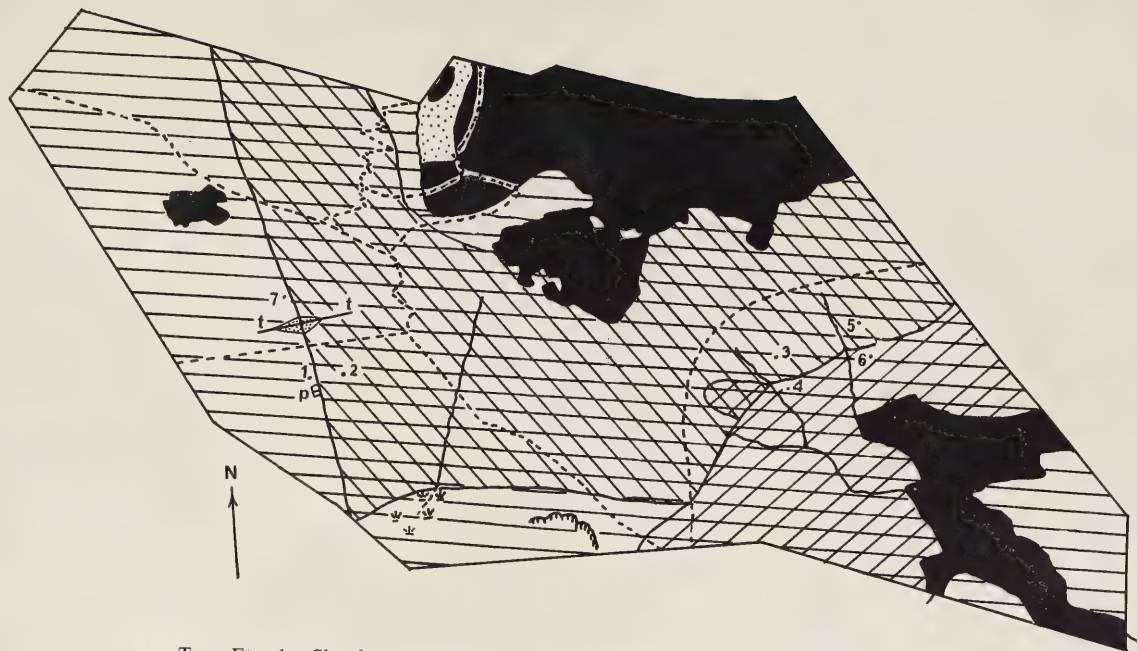
(i) *Cyrtanthus contractus*—by itself—a typical “fire lily” (pl. 1, fig. 1) producing flowering heads without the intervention of a leafy period, almost immediately after burning.

(ii) A group which regenerated vegetatively very quickly and flowered about a month later than *Cyrtanthus*, beginning in October, 1948. This consisted mainly of herbs but a few suffruticose subshrubs (hemixyles) are in this group (e.g. *Clusia heterophylla*).

(iii) A group which began to flower about a month later than group 2, commencing mid November to early December.

(iv) A group, mainly woody but including some herbs, which regenerated very slowly in the first year but flowered in the spring of 1949 or later.

(v) A group which was destroyed by fire and regenerated solely from seed, e.g. *Selago corymbosa*, *Anthospermum aethiopicum*, *Erica chamissonis* and *E. demissa*, and *Cliffortia repens*. The two species of *Erica* did not begin to regenerate until 1950. *Erica* regenerates from seed brought in by the agency of wind, therefore a time-lag may occur especially if a poor seed season occurs after fire. *Anthospermum* has less time-lag than *Erica* and appears so widespread that one assumed it to regenerate from dormant seed present in the soil (Levyns, 1935, showed it to be still 59% viable after 5 years). The fact that seed of *Erica* must fall on the surface, whereas *Anthospermum* may start off from buried seed, probably makes *Erica* more susceptible to drought. The obligate mycorrhizal relationship of *Erica* may also be involved. Attempts to germinate *Erica* seed



TEXT FIG. 1.—Sketch map of Reserve showing approximate areas burnt in 1948 (\\), 1951 (///), and 1955 (≡); also sites (1—7) of soil thermometers, the positions of the experimental plots (*p*), the unburnt areas left in 1955 (---), and the transect (*t*). Not all to true scale.



FIG. 1.
Cyrtanthus contractus in flower ca. 20 days
 after fire. Note flowers damaged by grazing
 (typical of viet rat damage to buds).

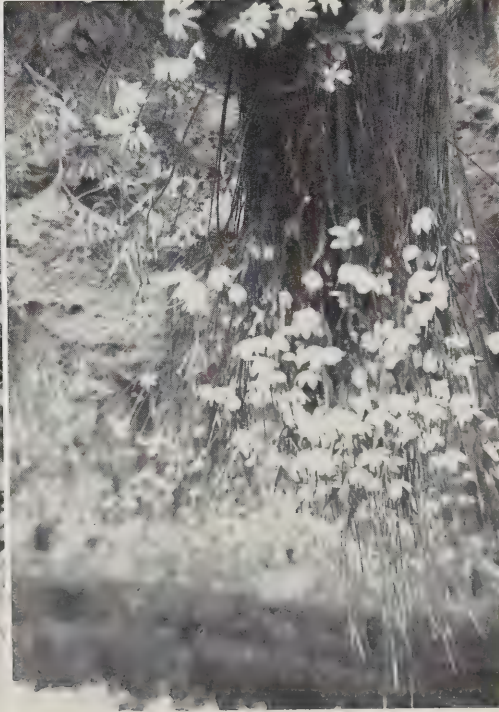


FIG. 2.



FIG. 3.

Characteristic massed flowering of *Bobartia burckellii*
Tarchonananthus camphoratus, showing epicomitic regene-
 ration typical of many forest and scrub species.
 of *Berkheya decurrens*.
 in 1951 and 1955. Also present: *Senecio concolor*, leaves
 1949 or 1950, but flowered profusely on areas burnt
 (November, 1948). *B. burckellii* did not flower at all in

in Petri dishes led to failure, but in pots of natural soil a high germination rate was achieved.

The system of life forms employed throughout the paper is that of Raunkiaer, modified for shrubs and suffrutices according to the system of Du Rietz (1931).

A close relationship has been demonstrated (Martin l.c.) between the life-form (aeroxyle or geoxyle) and the type of regeneration. Silhouettes of some typical nanophanerophytes of the Reserve are shown in text fig. 2.

TABLE I

Regeneration In Heath After Burning, August 15th, 1948.

	Type in subsequent years.	Raunkiaer Life Forms.
Group I. First seen flowering 1st Sept. 1948.		
<i>Cyrtanthus contractus</i> (Plate 1 fig. 1.)	1	Gb
Group II. First seen flowering 24th Oct. 1948.		
<i>Acalypha peduncularis</i> (Text fig. 6)	2	Gt to H
<i>Anemone caffra</i>	1	Hsr
<i>Clutia heterophylla</i>	1	Ch to G
<i>Eragrostis capensis</i>	1	Hr
<i>Gerbera viridifolia</i>	1	Hr
<i>Hypoxis obliqua</i>	2c	Gt
<i>Senecio concolor</i> (Plate 1 fig. 2)	2c	Hsr
<i>Tulbaghia alliacea</i>	2a	Gb
Group III. First seen flowering 28th Nov. 1948.		
<i>Ajuga ophrydis</i>	2a	Hsr
<i>Anisotoma mollis</i>	2c	Hsr
<i>Berkheya carduoides</i>	2b	Hsr
<i>B. decurrens</i> (Plate 1 fig. 2)	2b	Hsr
<i>Bobartia burchellii</i> (Plate 1 fig. 2)	1	Grh
<i>B. indica</i>	2a	Grh
<i>Diplopappus asper</i>	2b	Hr
<i>Helichrysum appendiculatum</i>	2b	Hsr
<i>Poa binata</i>	2a or b	Hc
<i>Scabiosa</i> spp.	2c	Hsr to Ch
<i>Senecio othonnaeflorus</i>	2a	Hr
Group IV. First seen flowering 30th Oct. 1949.		
<i>Chironia melampyrifolia</i>	4	Ch sb
<i>Helichrysum felinum</i>	3	Hsr
<i>Hermannia flammea</i>	3	Ch
<i>Restio triticeus</i>	3	Grh
<i>Sebaea macrostigma</i>	?	Hsr
<i>Themeda triandra</i>	3	Ch g
(In this group are included shrubs such as <i>Metalasia muricata</i> and <i>Tephrosia grandiflora</i> , where these survive fire. Some did not flower before 1950; Table II)		
Group V. Regenerating only by seed and not flowering before 1949 or later.		
<i>Anthospermum aethiopicum</i> (Text fig. 2)	4	N
<i>Cliffortia repens</i>	4	N
<i>Erica chamissonis</i> (Text fig. 2)	4	N
<i>E. demissa</i>	4	N
<i>Selago corymbosa</i>	4	N

When the drought of 1947-9 ended in the spring of 1949, it was at once noticed that even a year after the fire flowering was much more profuse on burnt than unburnt areas of the Reserve. The flowering of some spring-flowering species was advanced by as much as 14 days (i.e. in flower in August—early September on burnt areas while only in bud on adjacent unburnt areas), but more noticeable was the greater abundance of flowers. Although exact division into classes is always arbitrary, the flora could be divided into groups on this basis also:—

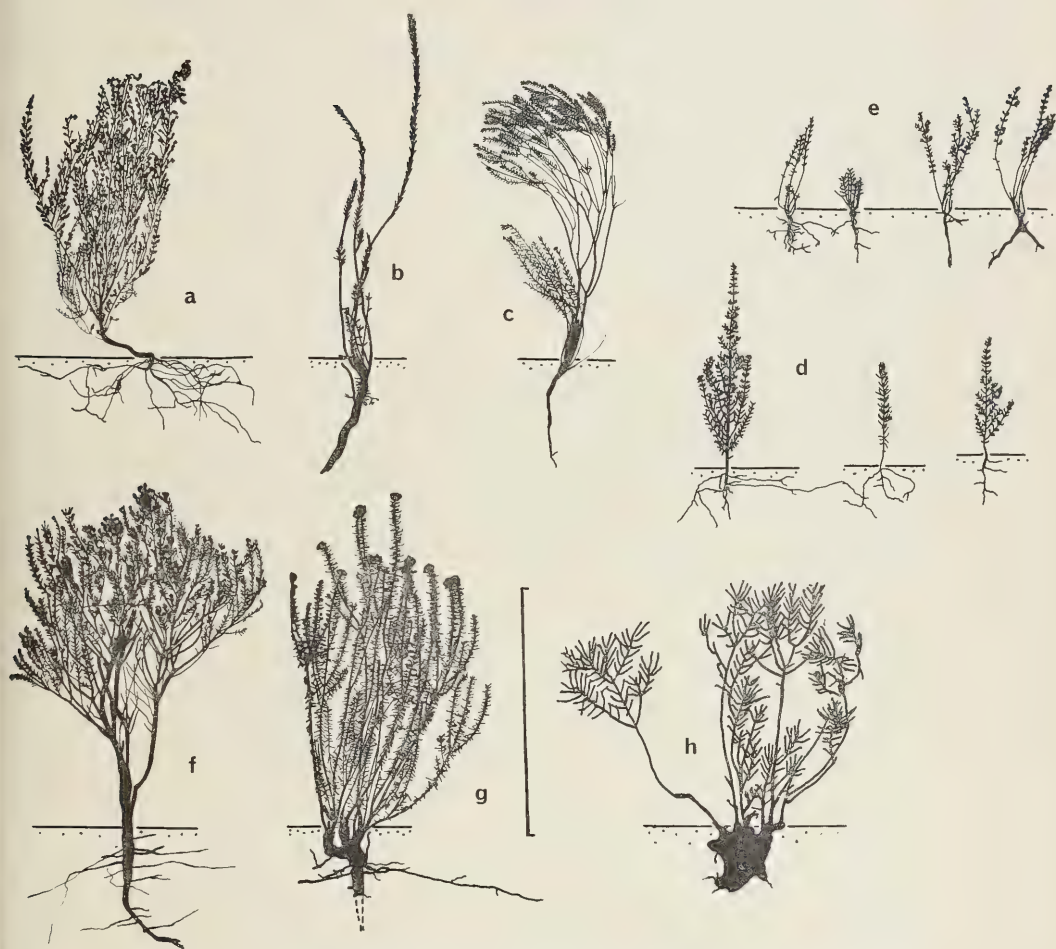
(i) Flowering shortly after fire, very rarely at other times, e.g. *Gerbera* spp.,

TABLE II
Life-forms and regeneration type of some woody plants in the Grahamstown Nature Reserve
1948-52.

Species	Root System where known	Life form (du Rietz Classification)	Seed establishment
<i>A. Regenerating Vegetatively From Base</i>			
<i>Agathosma peglerae</i>	Thick deep corky & woody tap root	1. <i>Holoxylic</i>	Not seen.
<i>Berzelia intermedia</i>	?		Not seen.
<i>Leucadendron salignum</i>	Thick fleshy & corky ligno-tuber. (Text fig. 2)	Geoxylic erect	Not seen.
<i>Metalasia muricata</i>	Thick woody tap root (Text fig. 2)	sedentary dwarf*	Seedlings infrequent.
<i>Montinia caryophyllacea</i>	?	shrubs	Seed highly viable, but seedlings not seen.
<i>Phyllica axillaris</i> †	Deep woody tap root (Text fig. 2)		Seedlings infrequent.
<i>Psoralea pinnata</i>	Deep woody tap root, shallow laterals	*	Seed large, with dormancy. Seedlings produced in small nos.
<i>Struthiola argentea</i>	Complex woody fibrous adventitious system		Not seen.
<i>Cliffortia linearifolia</i>	Thick woody stock & fibrous laterals	Similar, semi-sedentary (weakly subuliferous)	Seedlings frequent in good conditions.
<i>Anthospermum paniculatum</i>	Small woody stock-like tap root with relatively well developed shallow laterals (Text fig. 2)	2. <i>Hemixylic</i> Geoxylic erect	Not seen.
<i>Erica cerinthoides</i> }		sedentary half	Not seen.
<i>E. glumaeiflora</i> }	Thick deep woody tap root (Text fig. 2)	shrubs	Seedlings rarely seen.
<i>Clutia heterophylla</i>	? Tuberous	Geoxylic semi prostrate	Not seen.
<i>Indigofera hiliaris</i>	? Tuberous	sedentary half shrubs	Not seen.
<i>B. Not Regenerating Vegetatively</i>			
<i>Anthospermum aethiopicum</i>	Thin long tap root, small laterals (Text fig. 2)	1. <i>Holoxylic</i> Aeroxylic erect	Seed with dormancy, establishing well.
<i>Cliffortia repens</i>	Shallow laterals predominate over tap root	sedentary	Establishes well by seed.
<i>Erica chamissonis</i> }	Shallow spreading laterals, no tap root (Text fig. 2)	dwarf	{ Seeds minute, establish very well under good conditions.
<i>E. demissa</i> }		shrubs	
<i>Metalasia gnaphalodes</i>	Long woody tap root, & laterals (Text fig. 2)	Similar but (?) sometimes	Seedlings rarely seen.
<i>Ursinia anethoides</i>	Thin long tap root, small shallow laterals	geoxylic	Seedlings infrequent.
<i>Psoralea spicata</i>	?	Similar, true long-shoot shrub	Seed dormancy, establish well after fire.
<i>Selago corymbosa</i>	Shallow thin tap root & laterals	2. <i>Hemixylic</i> Aeroxylic erect sedentary half shrub	Establishes well from seed.

* May reach size of small tree elsewhere.

† Regenerated poorly in 1948, during drought.



TEXT FIG. 2.—Silhouettes of some shrubs showing root systems and aeroxylic (A) v. geoxylic (G) life-form: (a) *Erica chamissonis* (A), (b) *Erica cerinthoides* (G), (c) *Phyllica axillaris* (weakly G), (d) *Anthospermum aethiopicum*, 6mo., 12 mo., and 18 mo. seedlings (A), (e) *Anthospermum paniculatum* (G), (f) *Metalasia gnaphalodes* (A), (g) *Metalasia muricata* (G), (h) *Leucadendron salignum* (lignotuber G).

Clutia heterophylla, *Cyrtanthus contractus*, *Bobartia burchellii*, (Pl. 1, fig. 2) *Graderia scabra*.

- (ii) Similar behaviour to group 1 after fire, flowering less frequently subsequently.
 - (a) Those showing a strongly stimulated effect only in the year of burning.
 - (b) Those in which the effect diminishes slowly over two or three years.
 - (c) Flowering readily in unburnt areas but showing a stimulated effect after burning, e.g. *Senecio concolor*, (Pl. 1, fig. 2), *Scabiosa* spp.
- (iii) Flowering not occurring in the first year but more prolific in second and third years, e.g. *Themeda triandra*, *Restio triticeus*.
- (iv) Flowering not occurring after burning and not noticeably stimulated in subsequent years—seen in many shrubby spp. where these survive fire, e.g. *Phyllica axillaris*.
- (v) Flowering apparently unaffected by burning, e.g. certain autumn and winter flowering species, e.g. *Dierama pendulum*, *Leonotis leonurus*.

Geophytes and hemicryptophytes are generally stimulated and fall in groups 1 & 2. They either behave as long-day plants, or are day-length indifferent. Chamaephytes and herbaceous phanerophytes capable of regeneration from the base or from below ground may be of several types but group 3 is perhaps the most typical. Shrubby plants are mostly of group 4. Group 5 are short day plants of various life forms.

(2) QUADRAT DATA.

The quadrat data (Table III) were from the burnt and unburnt areas in the spring and summer of 1949–50, a year after the burning. By this time, as shown above, a number of species had reappeared which had not regenerated immediately after the fire, perhaps, in many cases, through dormancy because of the drought, or owing to a natural slowness of growth.

The quadrats, 1 m. square, were thrown at random in the burnt and unburnt heath, the only selection exercised being to distribute them roughly in two lines about $\frac{1}{2}$ mile long on opposite sides of the edge of the burn. Thus each quadrat in unburnt heath had an approximate pair in the burnt heath. The number of individuals of each species in each quadrat was counted. The comparison, however, between the two sets must be viewed in the light of the very definite non-random dispersion of species, as illustrated for instance by *Metalasia gnaphalodes* which with a frequency of 8 and density of 166 in the unburnt heath was clearly very much over-dispersed. Its apparent absence from burnt heath, could not therefore, without supporting evidence, be taken to imply poor regenerating power, but might be a result of insufficient sampling.

The absence of the grass *Elyonurus argenteus*, a species apparently without marked over-dispersion, seems to imply its destruction by fire or else very delayed vegetative regeneration. Other grasses, however, have spread. Of these,

TABLE III

Frequency and Density of Species in Quadrats, Burnt and Unburnt Areas 1949-1950

Species	Burnt Area		Unburnt Area	
	Fr.	No/ 25 sq.m.	Fr.	No/ 25 sq.m.
Pteridophyta				
<i>Pteridium aquilinum</i>	24	79	—	—
Coniferae				
<i>Pinus</i> spp. saplings	4	1	—	—
Gramineae				
<i>Aristida galpini</i>	24	51	28	10
<i>Alloteropsis semialata</i>	36	42	64	58
<i>Cymbopogon marginatus</i>	12	11	20	13
<i>Brachiaria serrata</i>	12	30	20	10
<i>Elyonurus argenteus</i>	—	—	36	29
<i>Eragrostis capensis</i>	28	15	16	8
<i>E. curvula</i>	28	14	12	6
<i>Eulalia villosa</i>	20	15	24	14
<i>Harpechloa falx</i>	12	20	24	20
<i>Pentstschistis augustifolia</i>	12	6	16	17
<i>Panicum perlatum</i>	36	53	8	8
<i>Setaria flabellata</i>	4	240	12	23
<i>Sporobolus capensis</i>	28	10	12	3
<i>Themeda triandra</i>	56	120	80	88
<i>Tristachya hispida</i>	11	7	24	17
Cyperaceae				
<i>Bulbostylis</i> sp.	8	22	—	—
<i>Ficinia</i> spp.	42	48	8	16
<i>Schoenoxiphium sparteum</i>	72	87	40	48
Other Monocots				
<i>Aristea pusilla</i>	32	10	16	11
<i>Bobartia burchellii</i>	8	2	24	41
<i>B. indica</i>	12	15	28	11
<i>Hypoxis obliqua</i>	28	16	40	23
<i>Restio triticeus</i>	24	70	56	65
Compositae				
<i>Athanasia punctata</i>	—	—	24	17
<i>Berkheya carduoides</i>	36	88	32	12
<i>B. decurrens</i>	48	41	36	24
<i>Disparago ericoides</i>	8	2	16	20
<i>Gazania longiscapa</i>	32	14	4	1
<i>Gerbera piloselloides</i>	20	7	4	1
<i>G. viridifolia</i>	56	68	16	12
<i>Helichrysum anomalum</i>	4	2	24	16
<i>H. appendiculatum</i>	36	17	12	3
<i>H. felinum</i>	12	12	40	48
<i>H. nudifolium</i>	76	122	88	82
<i>H. subglomeratum</i>	36	73	72	110
<i>Metalsia gnaphalodes</i>	—	—	8	166

Species	Burnt Area		Unburnt Area	
	Fr.	No/ 25 sq.m.	Fr.	No/ 25 sq.m.
<i>M. muricata</i>	24	25	16	14
<i>Senecio concolor</i>	76	134	24	6
<i>S. othonnaeflorus</i>	64	78	52	73
<i>S. pterophorus</i>	24	28	—	—
<i>Ursinia anethoides</i>	—	—	16	47
Leguminosae				
<i>Amphithalea williamsonii</i>	—	—	8	5
<i>Indigofera</i> spp.	12	27	—	—
<i>Psoralea pinnata</i>	16	7	4	3
<i>Tephrosia capensis</i>	28	123	24	16
Other Dicotyledons				
<i>Acalypha peduncularis</i>	8	25	28	51
<i>Alepiea ciliaris</i>	28	12	72	46
<i>Anisotoma mollis</i>	20	12	8	2
<i>Anthospermum aethiopicum</i>	56	120	56	72
<i>A. herbaceum</i>	20	12	4	1
<i>A. paniculatum</i>	16	5	32	28
<i>Centella eriantha</i>	68	114	32	51
<i>Chaetacanthus setiger</i>	36	24	20	9
<i>Chironia</i> spp.	4	1	16	11
<i>Cliffortia linearifolia</i>	36	38	20	22
<i>C. repens</i>	8	18	8	11
<i>Clutia alaternoides</i>	—	—	8	5
<i>C. heterophylla</i>	20	11	36	20
<i>Erica chamissonis</i>	—	—	20	23
<i>E. demissa</i>	—	—	36	103
<i>Euphorbia striata</i>	24	7	—	—
<i>Gnidia sericea</i>	20	7	4	1
<i>Hibiscus aethiopicus</i>	28	25	32	8
<i>Oxalis</i> spp.	34	25	20	9
<i>Phyllis axillaris</i>	—	—	28	16
<i>Polygala hispida</i>	28	21	20	11
<i>Scabiosa</i> spp.	20	9	12	11
<i>Selago corymbosa</i>	24	31	4	3
<i>Struthiola parviflora</i>	28	21	4	3
<i>Thesium</i> spp.	22	12	8	2

Density Differences

	Burnt	Unburnt	Increase or Decrease	Change %
Total Pteridophyta	86	2	+ 84	—
Total Gramineae	712	369	+ 343	+ 93
Total Cyperaceae	161	69	+ 92	+ 132
Total other Monocotyledons	132	171	— 39	— 23
Total Leguminosae	189	60	+ 129	+ 245
Total Compositae	783	698	+ 89	+ 13
Total other Dicotyledons	553	622	— 69	— 11
Total all species	2616	1987	+ 629	+ 32

Setaria flabellata is interesting in having occupied certain small areas very effectively. *Themeda triandra* had dropped in frequency, but increased in density locally, this being quite a general trend. The fire had evidently destroyed some individuals completely, but those not destroyed regenerated vigorously. Thus over-dispersion is more typical of the burnt area. Taking the grasses as a whole, number of individuals counted as separate tufts approximately doubled, while few species have increased at all markedly in frequency. Cyperaceae, especially *Ficinea*, have behaved like the Gramineae. Monocotyledons other than these show very little numerical response. *Pteridium* is strongly over-dispersed and its absence from the unburnt quadrats is due partly to sampling deficiency. In unburnt heath, the fronds are scattered and it is rarely dominant. The results from the burnt area appear to illustrate its vigorous response to burning, numerous young fronds being formed. (The observations of 1956 to be discussed later, show the apparently contradictory results for *Pteridium* that may result from fortuitous distribution effects.)

Among Dicotyledons, Leguminosae and Compositae show numerical increases, that in legumes being chiefly due to *Indigofera stricta* and *I. hilaris* (early stages in regeneration of which could not be reliably separated) and *Tephrosia capensis*, while the Compositae show an increase in *Berkheya* spp., *Gazania*, *Gerbera*, *Helichrysum nudifolium* and *Senecio concolor*. *Senecio pterophorus* is of interest as being one of the few outside species which have successfully colonised the burnt area. This species is absent from unburnt heath, the seed source presumably being the *Senecio pterophorus* dominated areas in exotic pine forest along the top of the ridge. Dicotyledons, other than these two families, show a slight overall decrease, mainly due to the destruction of *Phyllica axillaris*, *Erica* spp., the legume *Amphithalea williamsonii* and the Composite *Ursinia anethoides*, though there has been some compensating increase in *Anthospermum aethiopicum*, *Selago corymbosa* and *Centella eriantha*.

Thus in general, species typical of grassland have been favoured at the expense of species of heath. This might have been even more marked had the drought been less intense, though the observations of section 3 show that *Amphithalea*, *Phyllica* and *Ursinia*, might have persisted and *Erica demissa* returned sooner, under moist conditions.

(b) Further burning on the Nature Reserve, 1951.

Grass and heath fire broke out on the Howisons Poort hills on 3rd August, 1951, and spread into the Reserve at the southern end near Howisons Poort road. It burnt across the Reserve, being halted by fire breaks and confined on

the whole between the lower forest patch and the old burn.

This was the first opportunity to visit the site of a fire immediately after it occurred. On the 5th August it was only observed that burning was almost complete and very little above-ground vegetation had survived. Bushes of *Rhus fastigiata* and other indigenous shrubs however were often only defoliated and scorched around their base, and very few appeared completely destroyed. A few bushes of the exotic *Hakea* which had escaped eradication were more thoroughly burnt and their opened refractory fruits were shedding seed.

Six days later, no rain having fallen in the meantime, grass had grown ca. $\frac{1}{2}$ —1 in. from the base of some tussocks, showing that generally death did not occur below the soil surface, though in a few places the tussocks appeared to have been completely killed. Probably the temperature of the fire varied locally.

By August 13th faunistic activity was noted in the burnt area. Round the bases of many of the burnt bushes, colonies of ants which had apparently survived the fire were active. A minute spider, spinning threads from tip to tip of the burnt stalks of grasses was noticed, the whole area being copiously covered by these fine threads; apart from the ants, this appeared to be the commonest animal in the area. Its webs were also seen on the recently cut paths, but were not observed frequently in the undisturbed areas. The ecology of this (unfortunately unidentified) spider seems worth further investigation. Fresh dung of vlei rats (*Otomys* sp.), very common in regenerating and mature vegetation, was absent here, presumably because these mainly herbivorous animals had nothing as yet to invite them into the burnt area.

Observations following this fire made possible an extension and a revision of the previous work. Firstly, it was noted that although the fire, aided by a strong westerly wind, burned up to the very edge of the area burnt in 1948, it hardly anywhere crossed this boundary, which still formed a natural fire break since the regeneration of the area during and since the drought had evidently not produced sufficient herbage or fuel to burn again. Where such burning did occur it was patchy and incomplete. The burning of experimental plots in 1950, to be described presently, had demonstrated that the fire proceeds through vegetation like a chain reaction; each unit of vegetation must be raised to the combustion point, when it ignites almost explosively. If these chains of heating and ignition break more often than they proceed, the fire becomes patchy or dies out. A succession of good growth years followed by drought will produce a more inflammable product than a succession of drought years, and it is probably impossible to burn the same heath at intervals of less than four years under average local conditions. A third variable in the "equation of combustibility" is the nature of the herbage being produced. Grassland for instance, because it produces a more uniform cover, might burn more frequently. The

fires of 1948, 1951 and 1955 have demonstrated that the scrub and woodland are very difficult to burn under any conditions.

The second feature demonstrated by the 1951 fire was the ability of some species to regenerate, either vegetatively or by seed, under conditions of good rainfall, though they failed in drought. Thus *Phylica axillaris*, *Amphithalea williamsonii* and *Ursinia anethoides*, which had appeared to be exterminated in the area of the 1948 fire, regenerated reasonably well in the area of the 1951 fire, while *Themeda triandra* and *Restio triticeus* which delayed regrowth in the former until 1949, regenerated more promptly in the 1951 area. The most impressive difference was seen in the behaviour of *Erica demissa* and *E. chamissonis*. These plants had flowered in the spring of 1948 despite the drought, but no germination took place except in a few particularly sheltered areas—along gully banks, in crevices and damp moss beds. In 1949 the intensity of drought was such that buds did not open and withered on the plants. Scarcely any flowering occurred. In 1950 flowering was normal, rainfall was good during the spring and seedlings began to appear in the area of the 1948 burn though not in the plots burned in 1950. *Erica* seedlings first appeared in these plots after the 1951 flowering season, showing that a one year delay is normal but two years is not. Regeneration of *Erica* on the 1951 burn was observed in 1952. The light seed was apparently wind-borne into the burnt area for distances as great as 300 to 400 yards in extreme cases.

The main area of unburnt *Erica demissa*—*E. chamissonis* heath had been confined by the two fires to an area about 300 yards wide and from top to bottom of the Reserve along its western margin (Text fig. 1). Reseeding of areas remote from this was due mainly to isolated plants which had survived on rocky outcrops, "nunatak"-like, untouched by the fires, and in some areas of its former dominance, due to the absence of seed sources, regeneration of *Erica* remained negligible even in 1952.

EXPERIMENTAL AND ANALYTICAL STUDIES

(a) **Burning of experimental plots.**

Since the original vegetation of the burnt part of the Reserve could only be guessed at, a small experimental burning was made in August, 1950, about the same time of year as the original burning. The objects were (a) to study the effect on nitrification and other bacterial processes, (b) to find what temperatures were reached at the soil surface and at a depth of a few cms., (c) to study the

effect of removal of brushwood on the temperature of the burn, and (d) to study the regeneration of a part of the Reserve, the former vegetation of which was accurately known, so that from it, some better idea of the former vegetation of the Reserve could be obtained.

(1) SELECTION AND TREATMENT OF PLOTS.

Owing to the danger of burning the whole of the remaining vegetation, only a small plot was chosen. It was divided into two 5 m. sq. sub-plots separated by a firepath 1 m. wide. From one of these as much as possible of the brushwood

TABLE IV

List of species occurring in experimentally burned plots

(Symbols in parenthesis are those used in figs. 5 and 8)

Dicotyledons		* = actually in plot	
<i>Alchemilla capensis</i> (Alc)	o*	<i>Helichrysum petiolatum</i>	1*
<i>Anthospermum aethiopicum</i> (A)	f*	<i>H. subglomeratum</i> (Hs)	f*
<i>A. herbaceum</i> (Ah)	r*	<i>Hermannia flammea</i>	o*
<i>A. paniculatum</i>	o	<i>Hibiscus aethiopicus</i> (Hi)	f-a*
<i>Argyrolobium stipulaceum</i>	o	<i>Hypericum lalandii</i> (Hy)	o*
<i>Berkheya carduoides</i> (Bc)	o-f*	<i>Indigofera polioles</i>	o*
<i>B. decurrens</i> (Bd)	f*	<i>I. sp.</i>	o-f*
<i>Burchellia bubalina</i>	o	<i>Lobelia tomentosa</i> (L)	o*
<i>Centella eriantha</i> (Cn)	r*	<i>Metalasia muricata</i> (M)	f*
<i>Chaetacanthus setiger</i> (Ch)	f-a*	<i>Ochna atropurpurea</i>	o*
<i>Cliffortia linearifolia</i> (C)	d*	<i>Oldenlandia amatymbica</i> (01)	o*
<i>C. repens</i>	l. f-d	<i>Oxalis smithiana</i>	o-f*
<i>Clutia heterophylla</i>	f*	<i>O. spp. (x)</i>	f-a*
<i>Crassula ericoides</i>	r*	<i>Pimpinella schlechteri</i>	f-a
<i>Disparago ericoides</i>	f*	<i>Pinus pinaster</i>	r*
<i>Dobrowskya scabra</i> (Dw)	r*	<i>Psoralea spicata</i>	l
<i>Drosera cuneifolia</i>	o-f*	<i>Rhus eckloniana</i>	o
<i>Erica chamissonis</i> (Ec)	f*	<i>R. fastigiata/pyroides</i>	o
<i>E. demissa</i> (d)	d*	<i>Rhynchosia totta</i> (Rh)	f*
<i>Gerbera piloselloides</i> (Gp)	o*	<i>Royena pubescens</i>	o
<i>G. viridifolia</i> (G)	f*	<i>Scabiosa anthemifolia</i> (Sb)	o*
<i>Gymnosporia angularis</i>	o-f	<i>Senecio concolor</i> (S)	f*
<i>Haplocarpha lyrata</i>	o-f*	<i>S. othonnaeflorus</i> (So)	o*
<i>H. scaposa</i>	o-f	<i>Struthiola macowani</i>	o-f
<i>Helichrysum anomalum</i>	r	<i>S. parviflora</i> (St)	o
<i>H. appendiculatum</i> (Ha)	o*	<i>Tephrosia grandiflora</i> (Tep)	o
<i>H. felinum</i> (Hf)	o*	<i>Thesium junceum</i> (Thj)	o-f*
<i>H. nudifolium</i> (Hn)	o*	<i>Thunbergia alata</i>	o*
Monocotyledons			
<i>Alloteropsis semialata</i>	f*	<i>Panicum perlatum</i>	o*
<i>Aristea</i> spp. (Ar)	o*	<i>Pentascistis angustifolia</i> (Ps)	f*
<i>Bobartia indica</i> (B)	l-a*	<i>Restio triticeus</i> (R, Rt)	a*
<i>Brunsvigia grandiflora</i>	o	<i>Satyrium membranaceum</i>	r*
<i>Eragrostis cf. curvula</i> (Eg)	l*	<i>Schoenoxiphium sparteum</i> (Sch)	f*
<i>Ficinia</i> sp. (F)	a*	<i>Setaria flabellata</i> (Set)	f*
<i>Hypoxis obliqua</i> (Hv)	f*	<i>Themeda triandra</i> (T)	f-a*
Pteridophyta			
<i>Pteridium aquilinum</i> (Pt)	l. f-l.a		

was removed. A permanent metre quadrat was placed in each sub-plot and the vegetation accurately mapped (Text fig. 5a).

The vegetation was dominated by *Erica demissa* and *Cliffortia linearifolia* which formed a dense community varying in height from 12 ins. to 36 or 48 ins., and averaging 24 in. Table IV is a list of the plants in or near the two plots. The list of Monocotyledons is incomplete, since at the time of listing very few were flowering and from the leaves it is very difficult to identify them.

In collecting the debris from the plot which was cleared, it was noticed that many of the still rooted stumps bore burn marks, and such marks were seen also on stumps throughout the area; the community was not completely undisturbed but had previously been burnt. Signs of former disturbance were also seen in the occurrence of chopped-out pine stumps and narrow overgrown paths.

The dead brushwood and debris from the plot amounted to 10 kilograms. From the 1 m. quadrat in this plot as much as possible of the finer litter was also removed. The combined brushwood and litter from this quadrat was 1 Kg. 20 gm. (Plate 2, Fig. 4). Most of the brushwood was recognised as *Erica demissa*, *E. chamissonis*, *Cliffortia linearifolia*, etc. The fine debris consisted of small sections of stems of *Erica* and *Cliffortia*, small sections of leaf and stem of *Restio* and *Bobartia*, leaves of *Erica* and *Cliffortia*, *Erica demissa* fruit capsules and grass leaves. Some 20 gm. of animal pellets were separated, ca. 2% of the total organic matter.

On a second metre plot outside the burnt area, clearing was attempted in the same way, the plot being chosen at random. A total of ca. 870 gm. of plant material was extracted; the components were the same as before, but animal pellets amounted to only about 12 gm. In both cases beetle elytrae or other insect remains amounted to ca. 0.1 gm., a not very significant part of the whole.

The average of these two quadrats, ca. 945 gm., suggests that a value of nearer a kilo/sq. m. is a better estimate than that obtained for the plot as a whole by less thorough collecting. In each quadrat the amount of debris extracted by careful sweeping after rough hand picking of coarser debris amounted to about $\frac{2}{3}$ of the total ca. 380 grms./m². A minimum factor of about $\frac{2}{3}$ by weight should be added to the value obtained by coarse picking and the figure for the plot might be as high as 23 Kg.

(2) RESULTS OF BURNING.

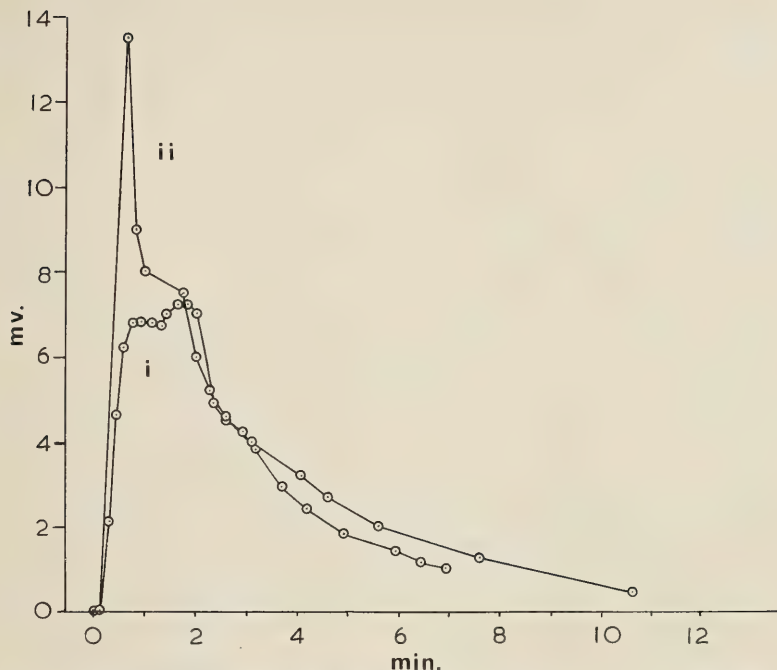
(i) *Method.* Brushwood, soaked in kerosene was ignited against the windward end of each plot. Fire spread into the plots and burned across them, fanned by a strong breeze. The surface temperatures were recorded with a

thermocouple and small capillary tubes filled with various organic compounds (Beadle 1940) were laid on the surface. In each case, care was taken to see that the thermocouple junction was in actual contact with the soil surface, though not covered. Sub-surface soil temperatures were recorded with melting point tubes only.

(ii) The uncleared plot burned easily and rapidly, except for a small patch in one corner. The fire burned forward both in the crowns of the plants and at the ground level, the crown fire preceding the surface fire by about a foot. The advancing margin may be likened to the advancing wave of a steady state chain reaction in which foci of combustion are formed at the same rate as they die out. The compounds in the melting point tubes at the surface were volatilised and the thermocouple measured a maximum e.m.f. of 13.5 mv. (corresponding to 550°C. Text Fig. 3). Crown temperatures were probably higher. Sub-surface soil temperatures however did not rise greatly, and menthol (melting point 43°C) at a depth of $\frac{1}{2}$ " did not melt.

The first attempt to ignite the cleared plot failed and extra brushwood was added. The fire then burned about half-way across before going out, and a third attempt was made. This time the fire burned across in the middle, leaving two unburnt patches on either side which were burned off separately with the aid of more brushwood. Even then the burning was not very complete, and the attempt to obtain uniform burning was abandoned. The thermocouple measured a maximum e.m.f. of 7.2 mv. (350°C) and the organic compounds in the surface series of tubes were melted but not completely volatilised; at $\frac{1}{2}$ " depth the temperature did not exceed 43°C. There seems little doubt that this difference in behaviour of the two plots was due to the removal of brushwood from the upper one. Actual temperatures recorded by the thermocouple will of course depend on the amount of combustible material in its immediate neighbourhood; such local differences might conceivably have been recorded on the same plot had more than one thermocouple been available, but the failure of the organic compounds in the tubes to volatilise on the cleared plot also indicates lower temperatures generally. The vegetation on the cleared plot was less tall, but this was made up mostly in stem height and combustibility depends much more on density of the crowns. Since the stems were not consumed, it seems unlikely that height alone was responsible for the difference.

The thermocouple readings show that temperatures did not remain high for more than 120 seconds at either spot. Half an inch of soil could thus form an effective insulator. The temperatures recorded above would not destroy living subterranean parts of plants, nor are they likely to have a marked direct effect on the soil and its microfauna and flora. Indeed, ants, thread-spinning spiders, etc. were noted abundantly active only two days after the fire, as they were later after the 1951 fire. The effect on protozoa and bacteria might be

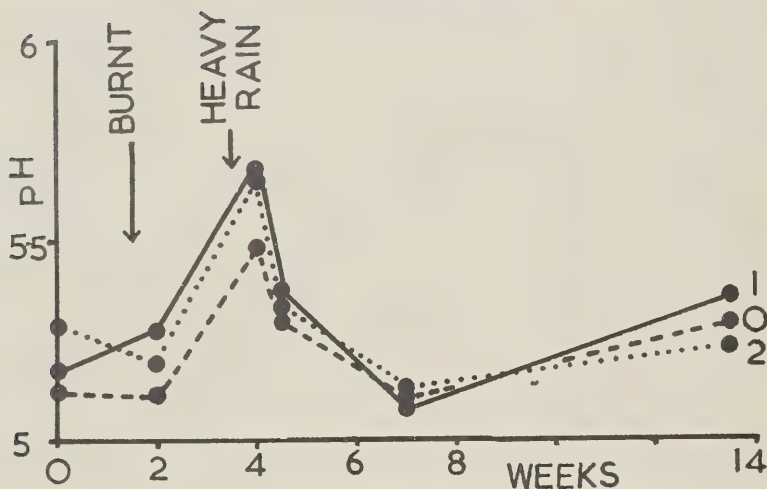


TEXT FIG. 3.—Surface temperatures (recorded in mv.) during burning of experimental plots: (i) cleared of brushwood and litter, (ii) not cleared.

to produce temporary encystment or spore formation. While no doubt mortality is widespread in the top $\frac{1}{2}$ " of soil, it will not be severe below this. The effect requires more careful investigation. There may be a possible association between destruction of superficial soil biota and the failure of strongly mycorrhizal species such as *Erica demissa* to germinate in the first season following burning.

Regeneration in the burned plots was studied by detailed plotting of the quadrats at intervals, the last examination being made in November, 1952.

The soil moisture and pH were analysed in the period immediately after the fire by taking samples from the corners of the quadrats. Fresh samples were taken at intervals from alongside the earlier ones for a 14 week period. However, no permanent change was observed in pH (Text Fig. 4). The sharp rises on some days are attributed to heavy rain which waterlogged the soil just prior to sampling. PH readings regularly changed in this way after rain, and were similar on the unburned control plot.

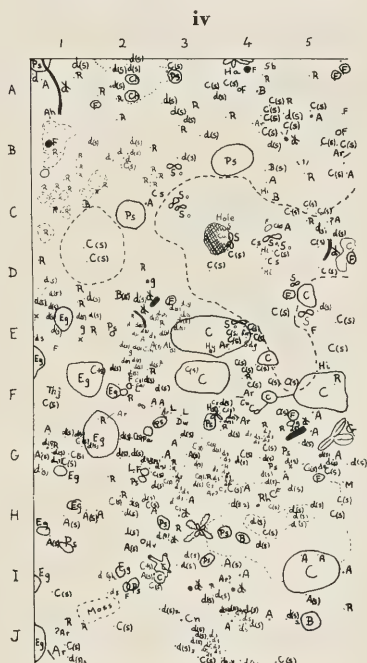
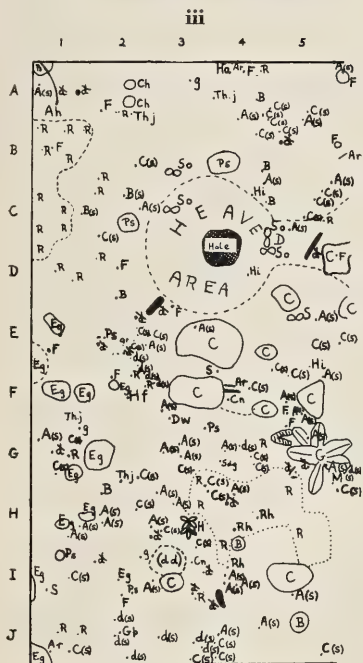
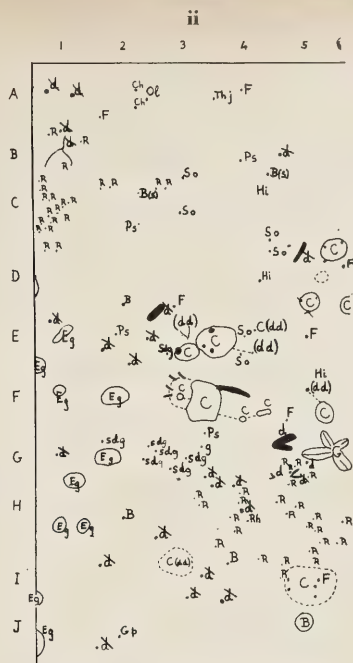
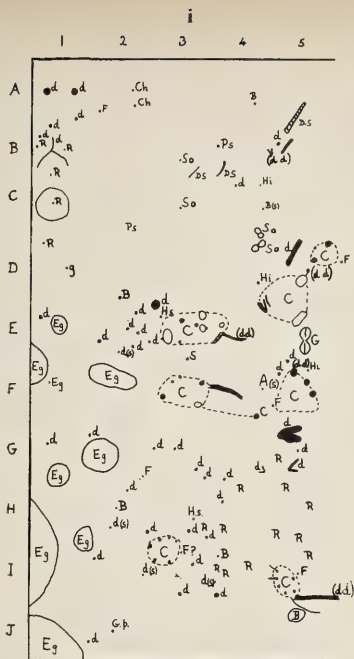


TEXT FIG. 4.—Course of pH changes in samples from corners of quadrats in plots. With the exception of the sharp temporary rise in all curves following heavy rain (probably a dilution effect), the changes over a 14 week period appear to be random. 0 = unburnt control, 1 = plot cleared of brushwood and litter, 2 = uncleared plot.

The maps of the quadrats need not be shown in full. A section of the quadrat on the cleared plot is shown giving the four sets of results (Text Fig. 5). This area is typical of both quadrats. However, some differences in regeneration were observed between the plots. Table V gives the numerical data for both the quadrats.

The most striking differences are firstly the difference in establishment of *Erica demissa* seedlings in 1951, when only 10 seedlings appeared in the uncleared quadrat compared with 55 in the cleared, and secondly the long-standing difference in establishment of grasses, which began to appear immediately after burning, some 200 apparent seedlings being established in the uncleared quadrat in 1950 and 1951, compared with fewer than 30 in the cleared quadrat. *Themeda* was confined to the uncleared quadrat, *Eragrostis* to the cleared one. As these differences may reflect initial differences between the plots rather than differences brought about by the clearing, they cannot be usefully discussed in great detail.

TEXT FIG. 5.—Part of mapped quadrat. Example is from plot cleared of brushwood: (i) before burning, (ii) 2 mo. after burning, (iii) 14 mo. after burning, (iv) 26 mo. after burning. Symbols are as in Table IV with the addition of the following: (dd) = dead, d = *Erica demissa* stump, g = unidentified grass (apparent seedling), Pa = *Parmelia*, (s) = seedling, sdg = unidentified seedling.



The similarities between the plots are of greater immediate interest. These similarities are (i) establishment of plants by seed is most marked for certain species:— *Erica* spp., *Anthospermum aethiopicum*, *Cliffortia linearifolia* and Gramineae. Only *Cliffortia linearifolia* regenerated well both from stocks and from seed. (ii) Once established, the shrub seedlings seem to have a high initial survival rate, *Erica demissa* averaging ca. 82% for the two quadrats, *Anthospermum* ca. 86%, *Cliffortia* 70% for the cleared quadrat and 56% for the uncleared. Gramineae however showed a survival rate (1951 to 1952) of 65% in the cleared quadrat (based on only 17 individuals) compared with 32% in the uncleared quadrat (based on 223 individuals). These counts are very crude, being based principally on coincidence of position and on increase in size between November, 1951 and November, 1952. Clearly these are maximum values, as no account is taken of seedlings established later than November 1951 and dying before the next census, or of false coincidences. On the other hand, it is unlikely that many seedlings would become established during the hottest summer months and *Erica demissa* in particular has a sharply demarcated flowering season and no seed dormancy, which would make establishment except in early summer very improbable. For this species, at least, it may be assumed that the survival values are fairly accurate. Except for *Erica* fewer obviously new seedlings appeared in 1952 than in 1951, which also suggests that most seedlings appear in the first year. (iii) Few seedlings of other plants appeared and values for survival have not been calculated. It is remarkable that so many of the hemicryptophytes (principally Compositae) and chamaephytes

TABLE V

Composition of Cleared and Uncleared Metre Quadrats on Plots Experimentally burned August, 1950

Species	1950 before burn		1950 after burn		1951		1952	
	Un- cleared	Cleared	Un- cleared	Cleared	Un- cleared	Cleared	Un- cleared	Cleared
<i>Erica demissa</i> (adult)	31	84	—	—	—	—	—	—
<i>E. demissa</i> (seedlings)	1	13	—	—	10	55	114	303
<i>E. chamissonis</i> (adult)	1	—	—	—	—	—	—	—
<i>E. chamissonis</i> (seedlings) ..	—	—	—	—	—	—	6	1
<i>Anthospermum aethiopicum</i> (adult)	—	—	—	—	—	—	28	55
<i>A. aethiopicum</i> (seedlings) ..	10	2	—	1	30	62	4	10
<i>Cliffortia linearifolia</i> (adult) ..	17	16	13	17	14	17	13	18
<i>C. linearifolia</i> (seedlings) ..	—	—	—	—	45	137	103	98
<i>Themeda triandra</i> (adult) ..	4	—	2	—	3	—	14	—
<i>Themeda</i> (apparent seedlings) ..	—	—	—	—	11	—	—	—
Other Gramineae (adult) ..	18	18	7	10	10	20	74	28
Other Gramineae (apparent seedlings) ..	17	—	205	18	213	17	68	6
Cyperaceae	13	6	12	8	22	22	15	32
<i>Bobartia</i> spp. (adult)	7	8	7	7	7	10	14	12
<i>Bobartia</i> (apparent seedlings) ..	—	—	—	—	7	3	4	5
<i>Oxalis</i> spp.	19	—	—	—	35	—	59	4
Compositae	5	7	8	—	—	—	—	—
Restio	7	14	2	14	23	20	28	22
Leguminosae	—	1	—	—	1	40	4	127
Miscellaneous (adult)	19	15	20	23	46	32	27	37
Miscellaneous (apparent seedlings)	—	2	—	14	—	6	19	18
Total individuals	170	186	278	168	457	445	594	778

represent fire survivals. In the majority of instances where a seemingly new plant appeared, this would be found on closer examination to have sprung from a pre-existing, often apparently dormant, root-stock. A difficulty in assessing the number of true seedlings is the impossibility of deciding without dissection from the soil, whether a given plant represents an individual or a sucker produced from another adjacent plant. Besides many Compositae, *Graderia scabra*, *Hibiscus aethiopicus* and *Clutia heterophylla* are probably mainly formed from such subterranean stocks or tubers. Text fig. 6, representing an individual of *Acalypha peduncularis* dissected from the soil, illustrates the great difficulty one would have, without total dissection, of identifying individuals of species with this type of life form. In practice, only the observation of cotyledons could be accepted as clear evidence of the seedling nature of individuals.

The data from the two quadrats, in conjunction with the data from the 1956 transect in the same area, give a fairly clear picture of regeneration after burning. *Cliffortia linearifolia* is hardly affected apart from the death of a few moribund stocks, and is increased by the establishment of suckers and of seedlings from dormant seed. However, many of these must die eventually as no great increase in numbers occurs. *Anthospermum aethiopicum* adults are killed but regeneration is rapid from dormant seed and the young plants are already beginning to flower in the second year when 8 ins. high. This species probably reached its



TEXT FIG. 6.—Plant of *Acalypha peduncularis* dissected whole from soil. B = stem endings charred by 1951 fire; I = shoots referable to spring (Sept) 1951; II = shoots referable to spring 1952. In both growth periods shoots have proceeded in majority of cases from buds below the surface (geophytic behaviour). The difficulty of deciding the limits of an "individual" without dissection from the soil is well illustrated.

maximum importance between the third and the sixth year and is beginning to die off thereafter. Many in the transect were recently dead after 8 years of growth, during which they reached a height of 4 to 5 ft. *Erica demissa* and *E. chamissonis*, despite initial slowness, grow steadily, have a relatively low mortality rate, and a higher competitive efficiency than either *Cliffortia* or *Anthospermum*.

(3) NITRIFICATION STUDIES.

In view of the slight direct effect of burning, it is considered unlikely to be the cause of that type of increased flowering which may persist for two or three years after burning. It might be responsible for flowering in those plants such as *Cyrtanthus* which flower within 14 days, or those which flower for a few weeks after burning, and do not flower in subsequent years, but for these alternative explanation is possible. This problem should be susceptible to laboratory investigation.

Bacterial activity in a number of Nature Reserve soils was investigated by storing freshly collected sieved soils for 30 days at constant temperatures and moisture content. Nitrates were determined as in Part I (Martin 1964). The samples were classified as unburnt heath, heath burnt in 1951, heath burnt in 1950, heath burnt in 1948, heath cut over in 1951 and heath cut over in 1950. All but one sample were non-nitrifying (Table VI). The one weakly nitrifying sample differed considerably in pH from the other samples, and though it was from a recently burnt soil, it is questionable whether this was a result of burning since no change in pH of this magnitude was observed in the experimental plot of 1950 or any other burnt site. Excluding this sample, no indication of higher rates of nitrification in the burnt area appeared. Culture experiments using ammonium salts and nitrite were continued over several months, but bacterial activity was low. *Azotobacter* could not be isolated from those soils, the pH of which was below 6. The idea that rapid regeneration and flowering in some plants might be a response to increased nitrification seems not to be applicable to this area. That plants may obtain increased supplies of nitrate as a result of decreased competition is not denied.

A close similarity between the effects of burning and clearing was noted. (Plate 3, Fig. 5). Flowering and regrowth are promoted on bare areas cleared naturally by landslides or artificially in making footpaths, and firebreaks, and are less prolific on old firebreaks than on new ones. Nitrification on these sites is also low (Table VI, Nos. 16 & 17). Thus an effect of removal of vegetation seems implicated, rather than any special stimulus produced by fires. This could be either an effect due to removal of competition, or a physical stimulus due to removal of vegetation. Moreover, since regrowth usually proceeds from below ground, any such stimulus must be perceived by the buried parts of the plants.

TABLE VI
Nitrification In Some Burned, Unburned And Cut Heath And Grassland Soils
Stored Sept. 20th—Oct. 14th 1951.

Site & Vegetation Type	Nitrate in p.p.m. d.wt.		H ₂ O % d.wt.	Loss on ignition % d.wt.	pH
	Initial	Stored			
Unburnt Heath					
1. <i>Erica</i> heath (soil thermometer site 1)	0.9	1.5	10.2	4.2	5.55
2. <i>Erica</i> heath (soil thermometer site 7)	2.9	0.6	14.2	6.0	5.59
3. <i>Erica</i> heath (along side No. 17) ..	2.7	0.7	10.5	5.1	5.56
4. <i>Erica</i> heath	1.0	1.4	18.9	6.6	5.53
Newly burned area (1951)					
5. Formerly <i>Metalasia</i> heath	2.4	8.5	20.8	6.6	6.18
6. Former <i>Erica-Phylca</i> heath (site 4)	0.9	0.9	15.3	6.2	5.77
7. Rocky area (site 6)	5.1	3.9	20.9	12.2	5.55
Older burned areas (1948 & 1950)					
8. <i>Cliffortia</i> — <i>Anthospermum</i> (site 2) ..	0.7	0.3	9.3	4.1	5.52
9. Experimental Plots (1950) <i>Cliffortia</i> — <i>Anthospermum</i>	1.9	2.7	8.8	3.3	5.66
10. <i>Metalasia</i> —grass heath	3.7	0.8	19.3	3.9	5.89
11. <i>Phylca</i> —tall grass heath (site 3) ..	1.0	1.8	21.8	6.1	5.65
12. Close to site 6 (site 5)	1.1	0.5	15.5	10.6	5.57
13. Grassland on main ridge	2.3	1.2	15.2	4.5	5.94
14. <i>Anthospermum</i> heath	1.4	2.1	14.4	3.6	5.99
15. Mixed grass— <i>Restio</i> heath (near No. 14)	1.8	2.1	14.6	4.3	5.95
Cut over—unburnt					
16. Fire path around experimental plots	2.6	2.2	7.6	3.5	5.56
17. Path recently cut in <i>Erica</i> heath ..	3.3	0.5	14.3	5.6	5.72

(4) SOIL TEMPERATURE MEASUREMENT.

Soil thermometers were installed in suitable sites during the first weeks following the 1951 fires. The thermometers were encased in an outer glass tube with the bulbs in wax, and buried in a horizontal position at 4" and 1" depths on burnt and unburnt slopes. The sites were selected for similarity of aspect and slope, depth of soil and stoniness.

The following sites were chosen:—

- | | | |
|---|----|----------------------------|
| (1) In unburnt <i>Erica</i> at the western end of the Reserve | .. | } slope ca.12° |
| (2) In regenerating heath at the western end of Reserve | .. | |
| (3) In regenerating heath, central part of the Reserve | .. | } Slope ca.22° |
| (4) In newly burnt heath, central part of the Reserve | .. | |
| (5) In regenerating heath, eastern Reserve | .. | } Slope ca.25° |
| (6) In newly burnt heath, eastern Reserve | .. | |
| (7) Mature <i>Erica</i> heath, western end of Reserve .. | .. | } Slope 22°
aspect 212° |
| | | |

Unfortunately, mature unburnt heath and newly burnt heath could not be compared on similar sites, as these no longer existed. Nor could burnt and unburnt sites be compared on north-west facing slopes, for the same reason. Sites

3 and 5, though quite close together, differed in slope, aspect, depth of soil, stoniness and dryness of soil and in plant cover, site 3 being much moister and having deeper, less stony soil and a consequent heavier cover than site 5. Site 4, (Plate 2, Fig. 6), a little lower down the hillside but with the same slope, aspect and soil depth as site 3, was believed to have been dominated by similar vegetation originally (*Erica* spp. and *Phylica* with tall grasses), while site 6, at the same level as site 5 was a similar rocky shallow soil, with the same type of vegetation (*Erica* spp., *Metalasia*, *Psoralea polyphylla* and grasses). Sites 1 and 2 also seemed to be quite comparable. Site 7 in mature *Erica* heath on a 22° slope, facing c. 212°, is most comparable with sites 3 and 4.

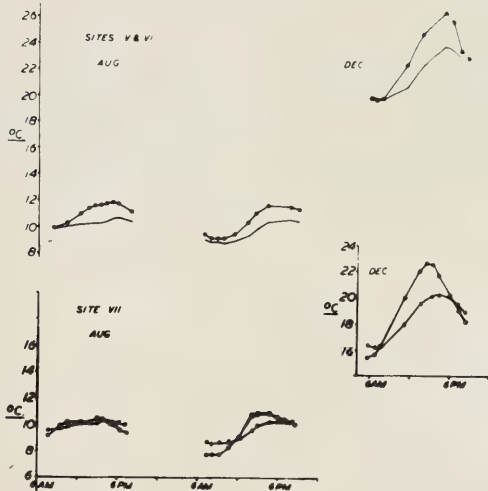
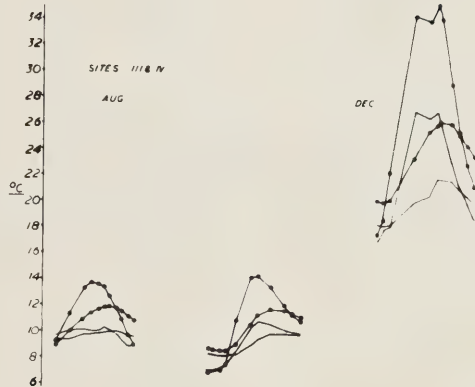
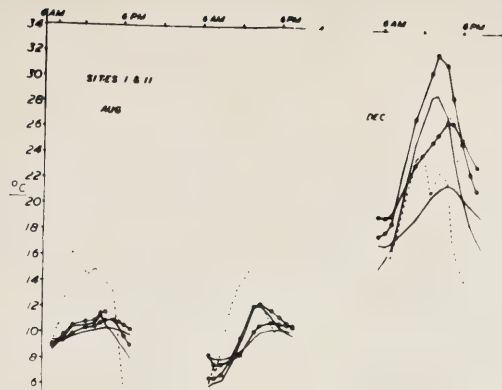
Scattered data were obtained in early August, 1951, for afternoons and evenings, indicating that daily maxima occurred before 4.30 p.m., even at 4" depth. Fluctuation in temperatures were more marked on burnt sites. The necessity for hourly readings was brought out, preferably for a 24 hour period, and this became possible on two occasions. On August 18th and 19th, 1951, under cool conditions of early spring, continuous readings were obtained for all the sites for two periods, one of 12 hours, and one of about 14 hours with a gap of about 10 hours between them. As temperatures were generally still dropping between 6 and 8 a.m. on August 19th it is safe to extrapolate across the gap. On December 1st a similar set of readings was obtained for a period of ca. 16—17 hours under conditions of summer. Unfortunately, all the days chosen were marred by cloud development, leading to a drop in air temperatures before the expected maxima were reached. Rain developed on the night of December 1st, so that a series of readings intended on December 2nd was abandoned.

The data are shown in text fig. 7. They show features which are usual in soil temperature curves, for example, the time lag of about 2 hours between the maxima at 1" and at 4"; a similar lag seems to apply to the minima. The inversions occurring in early morning and late afternoon indicate that at 4" depth the soil is relatively warmer during the night from about 6 p.m. until 7 or 8 a.m. in summer and from 5 p.m. until 9 to 10 a.m. in early spring.

Features special to these curves are the wide variation both between sites and at individual sites on successive days. On sites such as these with shallow rocky soils, variation due to soil depth, texture, moisture content and other variables must be expected and comparisons are legitimate only when made between the most similar sites.

The differences between mature *Erica* sites and burnt or cleared sites are what chiefly concern us. Despite a few curious features (the very flattened curves

TEXT FIG. 7. —Soil temperature runs for Spring (August) and Summer (December) conditions at sites 1 to 7. For explanation refer to text. Sites 5 and 6 had thermometer^s at 4 in. depth only. Air temperature.....



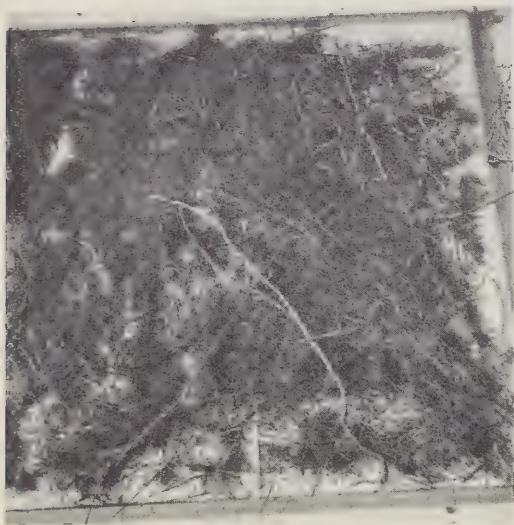


FIG. 4.
Brushwood and litter from one metre square on cleared plot. Dryweight 1020 gms.



FIG. 5.
Firepath effect. Mixed heath on left dominated by *Erica demissa* and *E. chamissonis* represents parent community. Pure *Cliffortia linearifolia* community on right is product of superficial clearing with incomplete removal of rootstocks.

Plate 2.

obtained on August 18th at all sites, compared with the more expected curves on the 19th, probably owe their character to some feature of the previous day's weather), the general character is the same throughout. In August a mature *Erica* soil reaches a maximum of 10.5°C at $4''$ and up to 12°C at $1''$, while adjacent regenerating heath reaches maxima of 11°C and 12.5°C respectively.

On newly burnt heath (site 4) maximum temperatures at $4''$ were as much as 12°C and at $1''$ 14.5°C , while in adjacent regenerating heath temperatures were 10°C and 12°C respectively. Site 7, unburnt, closely comparable with these, showed maxima of 10.5° and 11°C respectively. Minima likewise are lowest on burnt sites, 7°C on site 4 compared with 8°C on site 7. Sites 5 and 6 on steep slopes show similar features; maxima at $4''$ depth being ca. 1°C higher on newly burnt than on adjacent regenerating heath, though minima are similar.

Thus as far as the evidence goes, one may judge that even in early spring greatest extremes of temperature are experienced on burnt sites, next greatest on regenerating sites and least on mature heath sites. These results are to be expected and it is well known that vegetation cover decreases heat flow and therefore damps fluctuations of this sort. It is interesting to note that the dif-

ferences in maxima at this time of year are only of the order of 1 or 2 degrees. Taking the daily range, the fluctuations between minima and maxima are of the order 5 to 7°C at 1" at burnt site 4, and about 3.5°C on the adjacent site 3. On the other hand, mature heath and regenerating heat at sites 1 and 2 show very similar curves with daily fluctuations of about 6.5°C in each case on August 19th. It is clear that individual sites may vary considerably on account of differences in soil depth and humidity. Sites 1 and 2 are clearly drier than sites 3, 4 and 7 (Table V) and should not therefore be compared directly with them.

In summer the differences are much more extreme, the daily fluctuation at 1" being least at site 7 (8°C), then site 3 (10°C) and site 1, the driest and most



FIG. 6.

Soil thermometer site no. 4 in burnt area on 22° slope, showing general appearance of heath a few days after burning.



FIG. 7.

Result of 1955 fire. Island of unburnt heath, of which the left-hand side was burnt in 1948 and the right hand side about 1933. The dark colour of the 1955/33 burn is largely due to greater density and height of the still standing brushwood (mainly *Erica*), but also to the comparative scarcity of regenerating grasses (left foreground). Note tree composite *Oldenburgia arbuscula*, which survived fire on rocky ridge in background. The Pine trees in distance are outside the Reserve.

exposed, (13.5°C). On regenerating heath (site 2), the fluctuation was 15°C and on recently burnt heath (site 4) 18°C . At 4" depth, unburnt heath fluctuated less (3.5 to 5°C) compared with recently burnt (6 to 7°C), while on regenerating heath the more exposed site 2 fluctuated 7°C and less exposed site 5 fluctuated 4.5°C .

DATA RESULTING FROM THE FIRE OF 1955

The disastrous fire of August, 1955 was one of the most severe ever known in the Grahamstown district. Many square miles of heath, grass and plantation in the Grahamstown hills were destroyed. The extensive woodlands of Eucalypts, and self sown pines and Australian wattles were burnt right to the outskirts of the town. The whole of the heath and grassland of the Nature Reserve was burned. However, the natural forest and scrub, as in previous fires, escaped with marginal injury. In one or two places, roots ignited and smouldered for several days, spreading many yards into the forest with some consequent burning of litter, but no single area of natural forest was destroyed or even seriously burnt back, since the main components of the forest margin, *Rapanea melanophloios*, *Tarchonanthus camphoratus* etc. regenerate well by epicormic shoots (Plate 1, Fig. 3).

The experimental plots which had been last examined in 1952, were burnt shortly before they were due to be replotted. Further, since almost the whole of the remaining *Erica* heath was destroyed, the further development of heath in the Reserve could scarcely be compared with the past development, as no major seed sources remained within several miles.

Luckily, reburning on the 1951 burn was, predictably, slightly patchy and a few small clumps of regenerating heath plants escaped burning. Thus a small number of *Erica* seed foci remained in the Reserve, though they were now for the most part single isolated plants. In addition, chance had left one roughly lozenge shaped area of unburnt heath straddling the margin between the regenerating heath burnt in 1948 and the unburnt heath. This is indicated diagrammatically in text fig. 1 and depicted in Plate 3, Fig. 7. Unfortunately, as the author was leaving Grahamstown in 1956, the most could not be made of this opportunity of studying the stages of regenerating in detail within one small relatively uniform area. However, a belt transect 6" wide was run through the widest point of the lozenge and portions of this were plotted to scale on graph paper, showing the height and projective cover of all plants crossing the strip. A second transect crossing directly from the 1955 burn into the 1948 burn above the heath had to be abandoned through lack of time.

In Text fig. 9 which shows part of the results from the transect, arbitrary units are used, multiplying the projective cover by a factor derived from the height of the plant. Plants are grouped into six height classes (1) 0—2", (2) 2—4", (3) 4—8", (4) 8—16", (5) 16—32", (6) > 32". Thus a plant of projective

cover 12 sq. inches as measured with graph paper, and 9" high scores 48 units. In this way values were obtained which are related to herbage mass. Doubtless, plants of different life forms may have the same projective cover and height but a different herbage mass, but it is assumed here that for each species a series of values obtained in different years will give an indication of actual changes in herbage mass and hence of proportion of total plant mass in the community. This rather laborious method was resorted to as it was not deemed advisable to cut and dry-weigh the vegetation when so little undisturbed heath remained. It is assumed that the succession in space here also represents approximately the succession in time. Values are thus available for 0 years (1955), 1 year, (1956) 8 years (1948 burn plotted in 1956) and (?) 20 years in mature unburnt heath, as well as the twice burnt (1948/55) vegetation. Small strips of the transect plotted in elevation and plan are shown in Text fig. 8.

Some reservations must be made about the meaning of the graph. For instance, *Anthospermum aethiopicum* plotted in the eight year old heath was tall (up to 48" high) but mostly dead. It is clear that it reached its maximum cover a few years previously. The units attributed to *Anthospermum* in the 8 year old heath include only the living plants, the dotted line (A) represents the estimated units attributed to *Anthospermum* on the assumption that the dead plants had reached their maximum size in 1954.

The role of *Pteridium* in this transect is anomalous. Living plants were found only in the 8 year old heath. As *Pteridium* is seldom killed by burning at 8 year intervals, its absence in the area of the 1955 burn is most probably another phenomenon of overdispersion, i.e. its presence only in one part of the transect is fortuitous. *Pteridium* is therefore not considered further in this study.

The features which stand out most clearly are (a) Forbs reach their maximum vegetative mass in the first year or two after burning. (b) *Cliffortia* goes on increasing and appears to be close to its maximum at 8 years (probably a little earlier as the 8 year *Cliffortia* are already becoming leggy. (c) *Anthospermum* reaches its maximum between 1 and 8 years, probably between 4 and 6 years after burning and thereafter begins to die out. (However, seedlings develop and *Anthospermum* remains a component of the mature heath, though rather a minor one). (d) Gramineae are not important in the one year old burn of mature heath, nor do they assume importance later, though they are more conspicuous at 8 years than in mature heath. (e) *Erica demissa* and *E. chamissonis* seedlings first appeared in 1956, 1 year after the fire. Their mass is negligible at this stage as most are only $\frac{1}{4}$ " high. *Erica* appears to increase steadily in dominance to the mature heath. It is interesting that from 8 to 20 years, % bare ground appears to remain constant. *Erica* is increasing at the expense of its competitors during this period. The few other shrubs which enter include *Rhus fastigiata*, *Burchellia*

A detailed botanical illustration showing various plant species growing along a horizontal ground line. The plants are drawn in a sketchy, hand-drawn style. Above the ground line, there are several tall, thin plants with clusters of small flowers or fruits at their tips. Below the ground line, there are various leafy plants, some with small flowers. Labels are scattered around the plants, both above and below the ground line. Labels above include 'Fg', 'G', 'Sch', 'S', and 'Tsp'. Labels below include 'Gelb.', 'xL B.S.', 'B.S.', 'Calyx', 'R', 'CO', 'X', 'Y', 'Thj', 'Alen', 'Tf', and 'Bc'. Some labels are enclosed in circles or other shapes.

The figure consists of two parts. The upper part is a perspective drawing of a dune landscape. It shows a variety of plants: clumps of grass on the left, a tall, thin flowering plant in the center, and other smaller plants and grasses scattered across the dune surface. The lower part is a plan view (top-down map) of the same area. It uses letters and symbols to denote the locations of different plant species or vegetation types. Labels include 'T' (a large circle on the left), 'F' (several small circles), 'C' (a large circle in the center), 'R' (a small circle), 'Sch' (a circle on the right), and 'C(d)' (a circle on the far right). There are also dashed lines and other symbols like 'x', 'b', 'Hs', and 'P_s' indicating specific features or boundaries within the vegetation distribution.

The diagram below the sketch consists of several overlapping circles and labels. The labels include letters and numbers, some with subscripts or superscripts, and some with additional letters in parentheses. The labels are arranged in a way that suggests a hierarchical or spatial relationship between the different elements represented by the circles. The labels include: A(1), A(4d), A(4), B, C, C(1), C(5), C(10), C(11), C(12), C(13), C(14), C(15), C(16), C(17), C(18), C(19), C(20), C(21), C(22), C(23), C(24), C(25), C(26), C(27), C(28), C(29), C(30), C(31), C(32), C(33), C(34), C(35), C(36), C(37), C(38), C(39), C(40), C(41), C(42), C(43), C(44), C(45), C(46), C(47), C(48), C(49), C(50), C(51), C(52), C(53), C(54), C(55), C(56), C(57), C(58), C(59), C(60), C(61), C(62), C(63), C(64), C(65), C(66), C(67), C(68), C(69), C(70), C(71), C(72), C(73), C(74), C(75), C(76), C(77), C(78), C(79), C(80), C(81), C(82), C(83), C(84), C(85), C(86), C(87), C(88), C(89), C(90), C(91), C(92), C(93), C(94), C(95), C(96), C(97), C(98), C(99), C(100), C(101), C(102), C(103), C(104), C(105), C(106), C(107), C(108), C(109), C(110), C(111), C(112), C(113), C(114), C(115), C(116), C(117), C(118), C(119), C(120), C(121), C(122), C(123), C(124), C(125), C(126), C(127), C(128), C(129), C(130), C(131), C(132), C(133), C(134), C(135), C(136), C(137), C(138), 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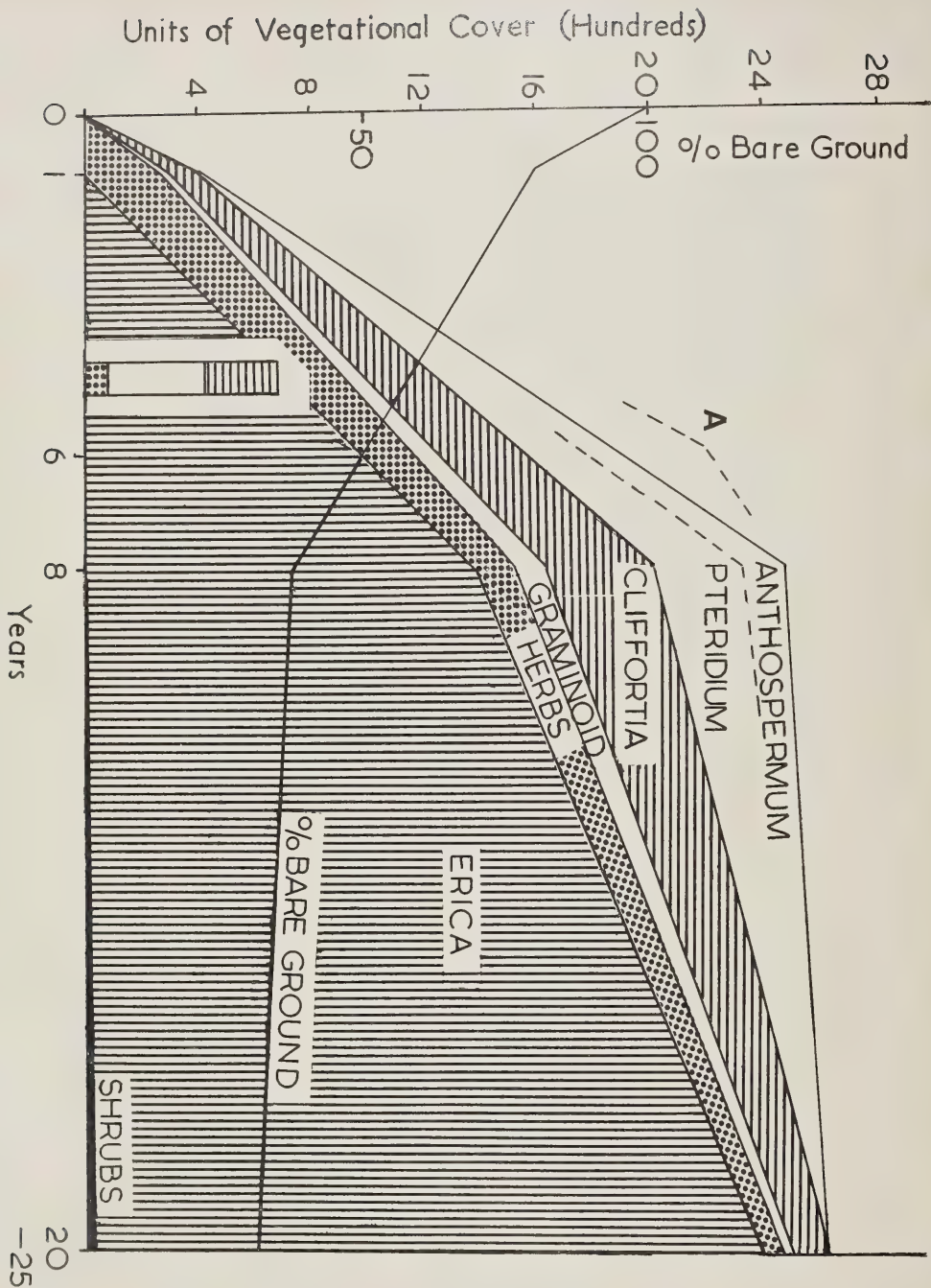
bubalina, *Myrsine africana*, *Psoralea spicata* and *Metalasia muricata*. Though apparent to the eye, they make very little showing in the transect.

The twice burnt heath has a very different appearance from the once burnt, though it is presumably derived at least in part from the community of which the 8 year regeneration heath forms the surviving example. The role of forbs is surprisingly much less and that of *Cliffortia* and grasses much more than in the 1 year old burn. The reason is perhaps that in the period 6—8 years after burning, grasses and *Cliffortia* reach their maximum cover, thus burning at this stage catches *Cliffortia* at a high level of physiological efficiency. Burning at 20 years finds *Cliffortia* in a senescent state. Perhaps the same is true of grasses, many of which seem to regenerate from subterranean buds rather than from seeds. The same argument cannot be applied to forbs, for if they are degenerate at 8 years, they should be even more so at 20 years, yet their regrowth from subterranean rhizomes and stocks in a vegetation type in which the above ground parts are scarcely apparent, is remarkable. One possibility is that we are dealing with a further case of non-random distribution. It is on this point that the second transect through the direct transition from once burnt to twice burnt heath could have thrown light. All that can be said is that the greater abundance of grasses in the twice burned area made the transition sharp even here (Plate 3, Fig. 7). It is probable that *Helichrysus* spp., especially *H. subglomeratum*, were fortuitously more abundant in the twice burnt area and that *Berkheya* spp. in the once burnt, and it may be that the apparent decrease in forbs is simply a product of the difference in rosette size of these spp. and the mode of representation employed, the rosettes of *H. glomeratum* being generally smaller, though it reaches the same flowering height.

DISCUSSION

The effect of fires on nanophanerophytic vegetation ("heath", "brush", "macchia", "sclerophyll scrub") has been described for many parts of the world. In the majority of cases, a marked increase in herbaceous cover, sometimes including grasses, has been reported. Jarrett and Petrie (1929) reported a prolific production of seedlings of both woody and herbaceous species in S.E. Australia. Pritchard (1951) upheld the view that fire should be regarded as part of the natural environment and is responsible for preserving species diversity in plant communities, especially as regards the herbaceous flora. The behaviour of chaparral has been discussed by Sweeney (1956) who reported numerous species

TEXT FIG. 8.—Specimen section of 6" belt transect plotted 1956 (a) burnt in 1955 after ca. 20 years of growth. (b) burnt 1948 and 1955. (c) burnt 1948 and showing 8 years regeneration. For corresponding transect in heath unburnt ca. 20 years see Pt. I (Martin 1964). Symbols in addition to those in text fig. 5 and Table IV: b = *Bryum* sp., B.S. = burnt stump (unidentified), E.s. = *Euphorbia striata* Hx = *Harpechloa falx*, Rs = *Restio sejunctus*, Sel = *Selago corymbosa*.



of annuals regenerating by means of dormant seeds surviving fire in the soil. He investigated the heat penetration of soil and the germination behaviour and heat tolerance of seeds, concluding that the vast majority of plant seedlings in chaparral burns are from viable seeds already in the soil when the fire occurred. He endorsed the findings of Pritchard and further concluded that the occurrence of herbaceous plants on burns is as characteristic of sclerophyll bush regions as are similarities in physiognomy of the woody cover. His findings differ from those in Eastern Australia however, where many of the seedlings are those of shrubs shed onto the ground subsequent to burning by species actually burnt in the fire but possessing refractory fruits (e.g. *Hakea* spp.), and from both South Africa and Australia, where annuals are of minor importance.

Adamson (1935) for the S.W. Cape region of South Africa reported only a weakly enhanced representation of annuals following fire in sclerophyll. He also reported the prolific increase of perennial shrubs (among them *Anthospermum aethiopicum*) for the first few years after fire.

The heath of the Grahamstown Nature Reserve is of a type generally classified as belonging floristically and physiognomically to the Cape "Sclerophyll" vegetation type of nanophanerophytic shrub heath. It exists under a rainfall of 25—30" p.a. with weak spring and autumn maxima. The present investigation differs from those of most other investigators in finding that the greater portion of the species becoming prominent and flowering soon after fire are hemi-cryptophytes, which actually survive burning by means of buds close to the ground surface. Geophytes and some chamaephytes (geoxylic hemixyles) also play a part in this regeneration but annuals are practically absent; plants regenerating from buried seed are mainly shrubs which only begin to become prominent in the second year after burning, while the seeds of the species which ultimately assume dominance are borne into the burnt area by wind. Such a type of behaviour by hemi-cryptophytes suggests that soil surface temperatures must be very low during fire, or that such plants are facultative geophytes. Both eventualities seem to be possible. Soil temperatures even $\frac{1}{2}$ " below the surface remained below 50°C in the experimental plots and a general survey suggests that this is quite usual. Story (1952) reports grasses regenerating from the base in *Erica brownleeae*-*Cliffortia paucistaminea* heath on the Amatola Mountains. This type of heath is taller, denser and produces a greater amount of inflammable brushwood than the Grahamstown heath, yet soil temperatures appear to remain relatively low. Recently Whittaker (1961) has made a similar report on North British Callunetum, which though not directly comparable with the

TEXT FIG. 9.—Herbage changes occurring in regeneration of heath after fire, using height—projective area data of type shown in text fig. 8 (see text). Inset = composition in 1956 of heath burnt 1948 and 1955.

community under review, seems to achieve the same range of surface temperature while burning. Cook (1940) records quite low subsurface temperatures from grassland burns in the Transvaal. The efficient insulation properties of even $\frac{1}{2}$ " of soil seem to be firmly established. Coupled with this are the adaptive life forms of some of the plants involved. *Helichrysum subglomeratum* and *Berkheya* spp. produce rosettes and short stolens or suboles which form new rosettes clustered round the initial plant. *Acalypha peduncularis* can behave facultatively as a hemicryptophyte or geophyte, and this probably applies to *Clutia heterophylla* which is structurally classified as a chamaephyte.

The belief of Sweeney (l.c.) that herb regeneration, like physiognomy, is a characteristic of the vegetation type requires qualification therefore. The precise form taken by herb and shrub regeneration may vary. In Australia, with its preponderance of woody-fruited Myrtaceae and Proteaceae, seed is commonly shed onto the soil after fire. In California the majority of herbs and shrubs seem to regenerate from seeds present in the soil. In South Africa Proteaceae behave much as in Australia. Most other shrubs regenerate from woody root-stocks or other subterranean parts, from seeds already in the soil or (in Ericaceae) by light seed blown into the area. The presence of lignotubers is frequent in Australia, occasional in South Africa and otherwise seems to be rare. Herb regeneration by seed is rather uncommon and annuals are practically absent in the Grahamstown heath investigated here. In these respects the Grahamstown heath is most comparable with the heath of the S.W. Cape.

The question of the status of heath requires some discussion. In Part I of this study *Erica demissa* heath is recognised as one climax type of the Witteberg region. The present study seems to confirm this from a consideration of the behaviour of *Erica demissa* after burning. The gradual assumption of dominance after burning is a process taking a period of about 10 years and the community is fully mature at 20—25 years of age. Story arrives at a very similar conclusion for the *Erica brownleeae-Cliffortia paucistaminea* community of the Amatolas, which in many respects resembles the *E. demissa-C. linearifolia* heath. The abundant herbaceous plants and chamaephytes in this heath can be interpreted in two ways. Either they represent a natural part of the vegetation which, however, is dependent on recurrent fires for its continued existence, or they may represent a former vegetation type invaded by heath and now present only as relicts. Most investigators of this type of vegetation have come to the former conclusion, either from a study of the life forms or from the succession. Thus Story (l.c.) reporting on the experimental enclosure made by Schonland in the Amatolas in 1922 and re-examined at intervals until 1949, concluded that *Themeda* grassland and *Helichrysum* veld were in seral relation to *Erica brownleeae-Cliffortia* "macchia", and that fire or grazing were responsible for preventing the spread of heath spp. Sweeney (U.S.A.) and Pritchard (Australia)

as quoted above, consider that fire must be regarded as entirely natural to these communities and that it is chiefly responsible for preserving the herbaceous flora which would otherwise become very much reduced. Wicht (1945) reached similar conclusions for the Cape flora.

Acocks (1953) appears to arrive at the opposite conclusions. His views on "fynbos" or "macchia" are only very briefly expressed, but from his maps 1 and 2 and the statement (l.c. pp. 14—15). "The fynbos shows the biggest movement of all, having spread from the neighbourhood of Bredasdorp, Montagu and Touws River to Grahamstown. It is now invading the Amatola Mountains", together with the following paragraphs, it appears that he believed the heath or fynbos of the Eastern Cape Province to be a "false macchia" i.e. one owing its existence to human interference. The comparison of maps 1 and 2 does not, however, literally express Acocks' belief. It is clear that patches of fynbos too small to be plotted on this scale could, in Acocks' view, always have existed east of Bredasdorp and Montagu. On no other basis could one account for the widespread endemism of heath species in areas as far east as Grahamstown.¹

The views arrived at in this paper are that the biological behaviour of *Erica demissa* and *E. chamissonis* is consistent with their interpretation as climax vegetation; that they and other heath dominants are not aggressive species likely to spread after human interference but rather the contrary; that the species diversity of the heath is not incompatible with the natural dominance of *Erica* and that the most reasonable explanation of the complex adaptive and adaptable life forms of many of these species is that they have evolved over many thousands of years under conditions in which natural selection has acted to conserve the most fire-tolerant adaptations. If *Erica demissa* and *E. chamissonis* are invading grassland following interference, it seems unusual that the adult plants unlike many of their competitors fail to regenerate from the base after cutting or burning, that the species are sensitive to drought, and especially that burning at more frequent intervals leads to increased abundance of grasses and extensive destruction of the *Erica* spp. The type of community

¹ Acocks (in lit. 1965), has offered very convincing reasons for believing that much of the heathy vegetation of the Eastern Cape is, in fact, "False Macchia", produced mainly by the agricultural methods of the past one and a half centuries. While agreeing with Acocks for some areas, and agreeing too, with much of the suggested mechanism, I consider the area described in this paper to have more of the character of a natural focal area from which indeed, some species now common in false macchia may originally have spread. It is clear that we both agree such focal areas must have existed. A history of false macchia for the Reserve and similar areas is rebutted. It is not claimed that the vegetation of the Reserve under observation in the period 1932-56, represents totally unmodified climax. It is, though, as nearly unaltered as we are likely to find, as is shown for instance, by the scarcity of so many false macchia species, e.g. *Elytropappus rhinocerotis*, of which only one or two plants were found on the Reserve, on obviously disturbed ground.

promoted by repeated burning is one in which Gramineae, herbs and small geoxylc shrubs are all prominent. Communities of this type in the Nature Reserve have been described in Part I as Grass Heath.

In terms of Whittaker's (1953) concept of the climax, the mosaic of communities in the area is a single climax pattern, with seral stages and various climax communities mixed, the varying degree of biotic influence forming a feature of the pattern. On the view of Tansley (1935), the *Erica* heath would probably be singled out as a climax type and the fire derived communities regarded as sub-climax communities of various sorts. Clement's terminology too, would regard the *Erica* heath as climatic climax, forest being postclimax, and grass heath a biotic dis-climax. There remain on the Reserve small areas of almost pure grassland, described in Part I, and it is clear that they do not fall among any of the communities described in this paper. At present the status of these communities cannot be decided. They may represent the effect of intensified grazing, either alone or with clearing. The fact that these grassy areas occupy some of the flattest ground in the Reserve may be significant, and it would be interesting to know more about the land utilisation and sites of buildings, kraals, etc., on the Reserve in the eighty years when it was used as farm land before it became commonage.

The third point of discussion—the nature of the stimulus to flower—is one about which no clear conclusions can be reached. In removing vegetation too many factors are changed for a field experiment to give a clearcut answer. Competition effects, temperatures and light effects, soil physical, biotic and chemical characteristics, may all be changed, some at once, some gradually.

In the present study, attention has been concentrated on certain types of response and on one particular stimulus, and it is suggested that irrespective of the precise temperature fluctuations involved, the change in diurnal rhythm after burning is one of the most important factors, if not the one major factor in the flowering behaviour of fire herbs such as *Cyrtanthus contractus*. These bulbous plants behave as if "triggered" by a simple release mechanism, and it is thought that in view of the quite small ephemeral temperature increases experienced at the depth of the bulbs, it is more likely to be the sudden change in daily temperature fluctuation that is perceived in what Sweeney calls a simple "stimulus-response relationship". Most other species affected by fires behave in a distinct seasonal pattern, similar in many cases to that which they show in unburnt heath. For these plants it is much more difficult to decide whether competition alone or soil temperature differences alone or some combination of these two, or even other stimuli, could be responsible. In a recent paper Specht (1963) has shown that phosphatic fertilisers may lead to increased and earlier flowering in S. Australian heath as well as an increase in herbaceous cover. The amount of phosphate liberated by burning of *Erica*, like that of

nitrate, must be too negligible to produce the observed effects, but the removal of competition for soil phosphate by roots of the dominants may be having somewhat the same effect on subordinate vegetation as fertilisation would have. It is, however, suggested that the possible role of increased diurnal temperature range and the generally higher daily maxima could be important and that these are factors often neglected in favour of competition.

CONCLUSIONS

1. The prolific flowering occurring after heath fires in the Grahamstown hills is due almost entirely to shooting from subterranean parts of surviving herbaceous plants.

2. The rapid transit of fire through heath, together with the insulatory properties of soil, results in only a momentary rise in surface temperature to above 500°C at any one spot, while temperatures at even $\frac{1}{2}$ " depth may remain below 50°C. Under these circumstances, perennating organs of plants can easily survive close to the soil surface.

3. Annual plants, regenerating from refractory seeds, often prominent in similar vegetation types elsewhere, are unimportant. Seedlings which appear in the first year after fire are mainly those of relatively slow-growing shrubs and perennial herbs, e.g. Leguminosae (Table III).

4. Flowering in the months following fire is in a definite order, repeated with little variation after each fire observed. This order is observed also in succeeding years though the abundance of flowering may fall off more or less gradually.

5. The same type of response is produced following clearing, suggesting a common stimulus in both sets of conditions. Addition of ash following fire is thus excluded as a major cause of flowering. Removal of competition, increased soil temperatures and increased diurnal temperature ranges are considered as possible causes. The flowering of "fire lilies" immediately after fire is considered to be a direct stimulus-response relationship, the putative stimulus being the changed rhythm of diurnal soil temperature fluctuations.

6. Any increase in nitrification following burning or clearing is regarded as negligible. pH changes are also negligible and variable.

7. Geoxylic shrubs, especially *Cliffortia linearifolia* survive fires and become temporarily dominant for a few years, later assuming a subordinate position becoming tall and apparently senescent.

8. A second group characterised by the aeroxylic *Anthospermum aethiopicum* and *Selago corymbosa* is destroyed by fire and regenerates from seeds present in the soil. *Anthospermum* also has a period of maximum importance in the regenerating heath and subsequently becomes a minor component.

9. A third group consisting of aeroxylic *Erica demissa* and *E. chamissonis* is destroyed by fire and regenerates entirely from light seed borne into the area subsequent to the fire. These two species under good conditions assume dominance by about 8 years after fire and subsequently are at a competitive advantage over all other heath components, through their production of a dense cover and extensive shallow root systems.

10. These species of *Erica* are sensitive to drought, do not seed well under drought conditions, and seedlings do not usually appear on a burnt site in the spring following a winter burn but late in the following spring. In drought conditions their appearance may be delayed.

11. Heath once burned will not readily burn again for several years. Burning of immature regenerating heath proceeds with difficulty and patchily, due to the incomplete cover and low supply of fuel. A very similar effect has been obtained experimentally in mature heath by complete removal of dry brushwood and litter.

12. Repeated burning of heath at relatively short intervals leads to a predominance of geoxylic shrubs and grasses and the total elimination of *Erica demissa* and *E. chamissonis*, resulting in the establishment of a "grass-heath complex".

13. On the other hand, prolonged absence of fire must result in some herbaceous spp. and possibly some shrubs becoming rare or disappearing. Irregular occurrence of fires appears to be essential to the maintenance of a diversified flora.

14. For the maintenance of the natural flora in the Grahamstown Reserve and Grahamstown Hills, the present trend towards more frequent (but probably more patchy) fires should be reversed, but no special effort to prevent fire completely need be made. On the other hand burning of very large areas at a time is disadvantageous for re-establishment of *Erica demissa* and *E. chamissonis*. Contained burning of heath at average intervals greater than 8—10 years, but not necessarily in excess of 20 years, seems to be consonant with the maintenance of all components of the present flora. These views are in general accordance with Wicht (1945).

15. The flora is regarded as having evolved over a long period in equilibrium with such an average fire interval. This conclusion is contrary to the suggestion that heath in Central Albany is a secondary community or "false macchia" which has replaced natural grassland.

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